

Female Sexual Receptivity Associated with Molting and Differences in Copulatory Behavior Among the Three Male Morphs in *Paracerceis sculpta* (Crustacea: Isopoda)

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Abstract. *Paracerceis sculpta*, a sphaeromatid isopod crustacean inhabiting the northern Gulf of California, forms harem polygynous breeding aggregations in spongozooids of intertidal sponges. Males in this species occur as three distinct morphs; α -males are large and possess modified uropods and telsons, β -males resemble females, and γ -males are small and inconspicuous. Females are semelparous, and sexual receptivity is associated with a terminal molt; the half-molted (sexually receptive) condition lasts 6–50 h. Field-collected premolt females do not contain sperm. Half-molted females possess sperm masses in both oviducts, and postmolt females contain sperm tails in their spent ovaries. The presence of an α -male does not affect the duration of female receptivity, but females can delay initiation of their reproductive molt if males are absent. Isolated premolt females are incapable of resorbing unispermated ova. Such females molt, but do not transport ova into their marsupium and die without reproducing. All three male morphs complete similar behavioral sequences during intromission. However, β - and γ -males copulate quickly and abandon females immediately after copulation, while α -males copulate longer and retain females after mating. The duration of female receptivity may encourage multiple mating and thus influence relative fertilization success among the three male morphs.

Introduction

The details of copulatory behavior are poorly known for most sphaeromatid isopods (see Bowman and

Kuhne, 1974; Buss and Iverson, 1981; Shuster, 1981). The dearth of such studies appears primarily due to the tendency for breeding pairs or harems of these animals to situate in cavities, burrows, or beneath benthic substrates (Menzies, 1954; Wieser, 1962; Glynn, 1968; Holdich, 1968; Jansen, 1971; Bowman and Kuhne, 1974; Eleftheriou *et al.*, 1981; Buss and Iverson, 1981; Shuster, 1981, 1987b; Upton, unpubl.). Direct observation of reproductive activities are, therefore, difficult or impossible for many species.

The timing of female sexual receptivity appears fundamental to the secretive nature of these isopods. In all sphaeromatid species examined to date, female receptivity immediately follows a molt (review in Ridley, 1983; Shuster, 1981, 1986). Most Crustacea are vulnerable to predators or mechanical damage in newly molted condition. Thus, in ancestral populations, females that preferred protected habitats prior to their reproductive molt may have enjoyed greater fecundity than females preferring more exposed areas.

The association of breeding females with sheltered locations may have facilitated male attempts to monopolize access to sexually receptive females (Emlen and Oring, 1977). Most female sphaeromatids lack sperm storage organs (Menzies, 1954; Ridley, 1983; Shuster, 1986), permitting males that mate first to place their sperm closest to a female's ova (Parker, 1970). Although the effect of mating order on male fertilization success has rarely been examined in Crustacea (Diesel, 1988), males that mate first achieve the greatest fertilization success in species with reproductive tract morphology similar to that of female sphaeromatids (Parker, 1970; Ridley, 1983). By guarding females prior to their reproductive molt, an-

Received 29 May 1989; accepted 15 August 1989.

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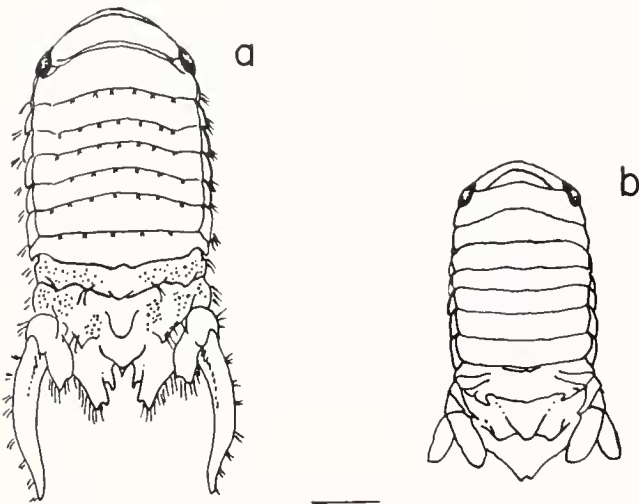


Figure 1. *Paracerceis sculpta* α -male (a) and premolt adult female (b). Horizontal line = 1 mm (redrawn from Brusca, 1980).

central male sphaeromatids may have enhanced their probability of mating first. Competition among males for mating priority is likely to have been intense in such species (Parker, 1970, 1978), and may have favored males capable of physically removing their mates from access by other males. An evolutionary history of male attempts to sequester their mates from reproductive competitors may have contributed to modern difficulties with observing breeding sphaeromatids (Shuster, 1981).

The timing as well as the duration of female receptivity can profoundly influence the intensity of sexual selection on males (Knowlton 1979; Shuster and Caldwell, 1989). Therefore, evolutionary analysis of male reproductive behavior must first consider how patterns of female sexual receptivity provide the context for male reproductive activities (Shuster, 1986). With respect to the characteristics of copulation itself, it is first necessary to determine when and how long females are sexually receptive, as well as how often, and with how many males, females are willing to mate.

In this paper, I report these details for *Paracerceis sculpta*, a sphaeromatid isopod crustacean inhabiting intertidal zones in the northern Gulf of California (Fig. 1). This species forms harem polygynous breeding aggregations in the spongocoels of *Leucetta losangelensis*, a common intertidal sponge (Shuster 1986, 1987a). *P. sculpta* males exhibit an unusual polymorphism involving three morphologically distinct types (Fig. 2, Shuster, 1986; 1987a, b; 1989). Alpha-males are larger than females, and possess robust telsons and elongated uropods. Alpha-males guard the entrance of spongocoels containing gravid females and defend their harems against other α -males. Beta-males are smaller than α -males, lack uropod and telsonic modifications, and resemble sexually

mature females in external morphology. Beta-males mimic female courtship behavior and enter spongocoels containing reproductive females by deceiving resident α -males. Gamma-males are smaller still, also lack telsonic modification, and use their rapid movements and small size to slip around the bodies of resident α -males and into spongocoels. Gamma-males, like β -males, prefer spongocoels containing reproductive females (Shuster, 1986, 1987a; 1989). The copulatory behavior of the three male morphs is presently undescribed.

Materials and Methods

Collection of experimental animals

Leucetta losangelensis sponges grow abundantly year-round in tidepools on the coquina limestone reefs at Playa de Oro and at Station Beach, approximately 3 km southeast of Puerto Peñasco, Sonora, Mexico (Shuster, 1986). Isopods used in experiments were obtained in collections of 50–200 individuals, made every 4 to 10-days between February 1984 and November 1985. Breeding aggregations of isopods were removed from spongocoels, placed in separate vials, and examined in the laboratory within 6 h of collection. Females were identified by the possession of mature ovaries visible through the ventral cuticle or embryos in the brood pouch. Males were identified by the presence of external genitalia and were classified as α -, β -, or γ -males by their body size and external morphology. Further details of collection and animal maintenance procedures, as well as details of male and female life histories, are available in Shuster (1986). All animals were returned to the Gulf of California after experiments were completed.

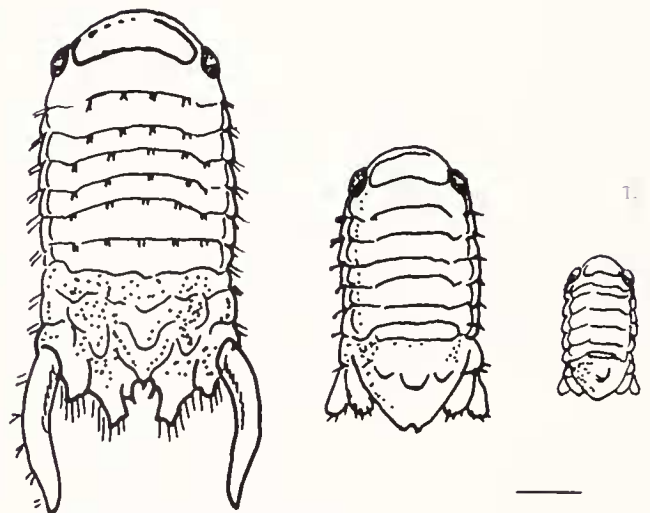


Figure 2. The relative body sizes of the three male morphs in *Paracerceis sculpta*. Left to right, α -male, β -male, γ -male. Horizontal line = 1 mm.

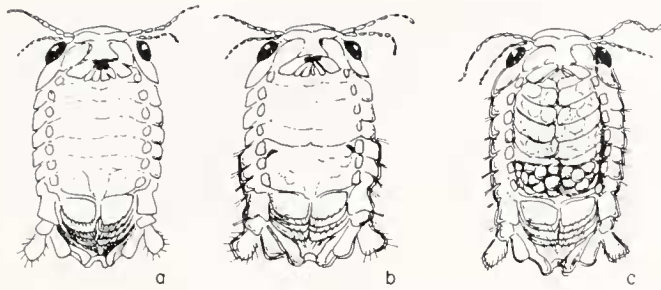


Figure 3. Diagram representing changes in female morphology associated with a sexual molt. Walking legs are not drawn. (a) Premolt female, (b) half-molted female (note genital pores in black at the base of the 5th leg), (c) postmolt female.

Sperm in the reproductive tracts of field-collected females

Females were removed from samples, measured to the nearest 0.15 mm using a stereomicroscope, and assigned to one of three categories describing their reproductive condition. Like many isopods, *P. sculpta* females undergo a biphasic molt that initiates their sexual receptivity (Ridley, 1983; Shuster, 1986). Females shed the posterior half of their cuticle below the fourth pereonal segment first, and several hours to several days later (see below) shed the anterior half of their cuticle. Unmolted females possessing mature ovaries were classified as "pre-molt" females (Fig. 3a). "Half-molted" females possessed mature ovaries and had shed their posterior cuticles (Fig. 3b). "Postmolt" females had completed their reproductive molts and transported their fertilized ova into their ventral marsupium (Fig. 3c). A more detailed description of female reproductive condition is provided in Shuster (1986).

Twenty females of each of the three reproductive conditions were chilled in a freezer for 10 min and then dissected in physiological saline under a stereomicroscope. The body cavities of half of the females were opened dorsally and the other half opened ventrally to permit examination of upper and lower aspects of the reproductive organs. Oviducts are transparent, and sperm, if present, are visible under low magnification (7 \times , Shuster, 1986). The presence or absence of sperm in the oviducts of dissected females was recorded.

Effect of α -males on the initiation and duration of female sexual receptivity

In nature, unmolted females are attracted to spongoceols containing α -males. Reproductive molting, mating, and brooding of young by females all occur within these spongoceols (Shuster, 1987b). To determine (a) the duration between female arrival in the spongoceol and

the onset of sexual receptivity, (b) the duration of sexual receptivity itself (*i.e.*, the half-molted condition), and (c) the effect of the presence of an α -male on the length of these durations, 40 unmolted females were removed from samples within 2 h of collection and placed in separate 225-ml cups containing food (*Amphiroa* thalli, Shuster, 1986) and seawater. A single α -male was added to 20 of these cups and each female was examined every 4 h until she had completed her molt.

Isolation of uninseminated premolt females

To determine whether sexually mature, but uninseminated females, were capable of resorbing ova for future reproductions, 14 unmolted females were maintained in 225-ml cups with food and weekly water changes until they died. All females were examined while undergoing their molts, and postmolt females were examined every other day for evidence of feeding, changes in cuticle condition, visible changes in the character of internal organs, and activity level.

The copulatory behavior of males

Copulatory behavior was examined by placing individual half-molted females into a watch glass containing seawater and introducing a single α - ($n = 8$), β - ($n = 3$) or γ - ($n = 5$) male. Interactions were observed under a stereomicroscope and, after apparent copulation, the genital pores and ventral surfaces overlying the oviducts of females were inspected under a stereomicroscope at high power (70 \times) for evidence of sperm transfer. To determine if females mate more than once, a half-molted female was placed in a watch glass, and four males were individually introduced to the female for 10 min each in the following sequence: α -, β -, γ -, α -. All behavioral interactions were recorded on tape.

Results

Sperm in the reproductive tracts of field-collected females

Premolt females contained no sperm in their reproductive tracts ($n = 21$, Table I). This is not surprising

Table I

The location of spermatozoa within the reproductive tracts of premolt, half-molt, and postmolt females collected from Leucetta spongoceols

Female condition	Sperm present			n
	In oviducts	In ovaries	No sperm	
Premolt	0	0	21	21
Half-molt	19	0	0	19
Postmolt	19	19	0	19

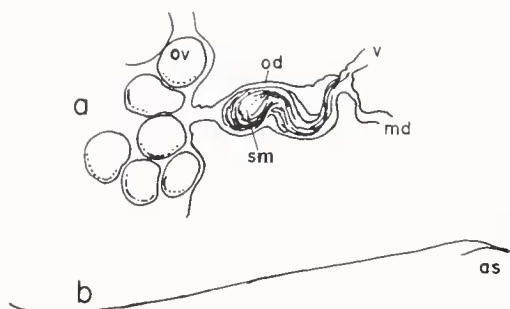


Figure 4. (a) Sperm in the oviduct of a half-molted female; (b) isolated spermatozoon; as = acrosome; md = portion of oviduct leading to marsupium; od = oviduct; ov = ovum; sm = sperm mass; v = vagina.

as the vaginae of premolt females are fused prior to the reproductive molt and are physically incapable of accommodating male genitalia (details of female reproductive morphology in Shuster, 1986).

All half-molted females collected in the field ($n = 19$) possessed a whitish sperm mass in each oviduct. As mentioned above, females possess simple oviducts, with no sperm storage organs (Shuster, 1986). The sperm masses of inseminated females were visible through the ventral cuticle and were located approximately 0.25 mm inside of this opening, directly within the lumen of the oviduct. Sperm in the oviduct formed a loosely organized bundle (Fig. 4a). Intact sperm are approximately 1–1.5 mm in length, consisting of a long tail and a flange-like acrosome that is clearly visible at $70\times$ (Fig. 4b). Within the reproductive tracts of half-molt females, sperm are non-motile.

Postmolt females transport ova through their oviducts and into ventral pouches that form the marsupium (Shuster, 1986). Spent ovaries form an H-shaped bag that lies over the brood pouches when viewed dorsally (details in Shuster, 1986). While no intact sperm were found in the reproductive tracts of postmolt females ($n = 19$), sperm tails, minus their acrosomes, were distributed throughout the spent ovaries and occasionally found within the oviducts.

The effect of α -males on the initiation and duration of female sexual receptivity

Premolt females retained with α -males molt significantly sooner than premolt females retained in cups alone (one-tailed U-test, $P = 0.008$). Premolt females isolated in cups molted about five days after capture (median = 126.3 h, range = 6.0–208.0 h, $\bar{x} \pm SD = 120.78 \pm 70.17$, $n = 20$), whereas premolt females retained in cups with an α -male molted about three days after capture (median = 87.0 h, range = 4.50–138.0 h, $\bar{x} \pm SD = 70.35 \pm 47.24$ h, $n = 20$). However, the duration of

sexual receptivity, *i.e.*, the duration a female remains in a half-molted condition, was unaffected by the presence of an α -male. Sexual receptivity lasted about 24 h for isolated females (median h as half-molt = 24.0, range = 6.0–50.0, $\bar{x} \pm SD = 26.34 \pm 10.17$, $n = 20$), as well as for females retained with an α -male (median = 25.0 h, range = 7.5–41.0 h, $\bar{x} \pm SD = 25.09 \pm 8.80$ h, $n = 20$; U-test, $P > 0.42$).

Isolation of uniseminated premolt females

Uniseminated females do not resorb their ova. Isolated premolt females undergo sexual molts normally, and cease to feed like gravid females (Shuster, 1986). However, uniseminated females do not transport ova into their brood pouches. Within a few days after molting, the unfilled brood pouches of isolated females become opaque and slightly distended. The oostegites become progressively shriveled in appearance and begin to project outward from the body, while the ventral pereon grows large and appears to fill with fluid. Ovaries become progressively more pale, and the ova within begin to appear fuzzy and indistinct. Over several weeks, the ova diminish in size, but with no corresponding improvement in the physical condition of females. In several cases, the empty brood pouches of females became infested with fungi and protozoa while the females were still alive, and in all cases, isolated females became sluggish, deteriorated in physical condition, and died within 81 days ($\bar{x} \pm SD = 49.36 \pm 19.90$, $n = 14$). This period is comparable to the adult longevity of females that become gravid and release normal broods (Shuster, 1986).

The copulatory behavior of males

In watchglasses, α -males did not seem capable of detecting half-molted females from a distance of more than a centimeter. However, when females swam within this distance, α -males became active and lashed their antennae vigorously. When α -males contacted half-molted females with one of their antennae or with one of their walking legs, they immediately grasped females, adjusted them into a ventral-to-ventral position with respect to their own body, and pressed first one and then the other of the females' genital pores to their own genitalia (Fig. 5). Before being grasped, and while males adjusted their positions, females moved actively and occasionally escaped from males. However, once face-to-face with α -males, females became quiescent and permitted males to mate.

Each intromission (two per female) involved insertion of both of the male's penes into each of the female's genital pores, followed by rapid pumping of the male's first two sets of pleopods. Median intromission duration for α -males was 30 s (range = 15–120 s, $\bar{x} \pm SD = 39.08$

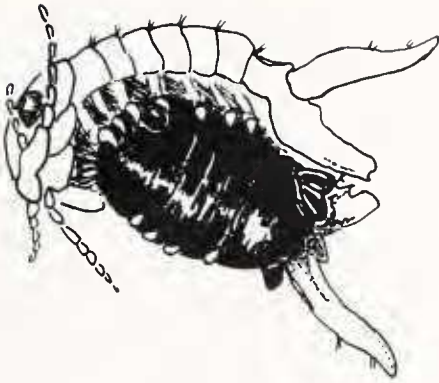


Figure 5. Alpha-male (white) in copula with half-molted female (black). Drawn from photograph.

± 28.43 s, $n = 13$) and the median duration of the entire copulatory sequence for α -males was 12.07 min (range = 4.40–19.92 min, $\bar{x} \pm SD = 11.59 \pm 4.60$ min, $n = 8$). In one case, an α -male completed the above sequence, retained the female, and copulated again, intromitting both of the female's genital pores. However, most α -males copulated as described above, and relaxed their grip on the female within 10 min after mating. Females became increasingly active following copulation, and shortly after α -males appeared to relax, females freed themselves and swam off. Females examined after single copulatory bouts contained sperm masses in both oviducts. These sperm masses appeared smaller than those routinely found in half-molted females collected in the field. On two occasions, females were left in the watch-glass with their α -male for an additional 4 h. Upon re-examination, both females found were embraced by their α -males, and both females contained sperm masses that appeared substantially larger than observed after their initial mating. Thus, females evidently mate more than once with an individual male.

Copulatory behavior involving females and β -males was similar in character to that observed between females and α -males. Beta-males grasped females and assumed a ventral-to-ventral position. Females became quiescent, permitted intromission, and were released by β -males almost immediately after mating. Median intromission duration for β -males was 62 (range = 30–79 s, $\bar{x} \pm SD = 54.83 \pm 20.26$ s, $n = 3$) and the median copulatory sequence duration was 2.97 min (range = 2.00–3.36 min, $\bar{x} \pm SD = 2.78 \pm 0.70$ min, $n = 3$). All females copulating with β -males contained sperm in both oviducts after a single copulatory sequence.

Gamma-males copulated, not by positioning females, but instead by climbing beneath them and positioning their own genitalia toward the females' genital pores. The mere contact of a male, not the act of being grasped and positioned, seems to stimulate quiescence, as females

paired with γ -males ceased moving soon after γ -males assumed positions beneath them. While α - and β -males rapidly moved their anterior pleopods during copulation and engage in few or no thrusting movements, γ -males thrust actively during copulation. Like β -males, γ -males abandoned females soon after mating. Median intromission time for γ -males was 42 s (range = 25–571 s, $\bar{x} \pm SD = 122.86 \pm 198.85$ s, $n = 4$) and median copulatory sequence duration was 5.75 min (range = 3.00–12.60 min, $\bar{x} \pm SD = 6.78 \pm 4.10$ min, $n = 4$), intermediate in duration between that of α - and β -males. All females mating with γ -males contained sperm masses in both oviducts. While intromission times for α -, β -, and γ -males were not significantly different (two-tailed Kruskal-Wallis test, $P > 0.05$), copulatory sequence times differed significantly among males (two-tailed Kruskal-Wallis $H = 7.96$, $P < 0.01$). Thus α -males evidently copulate longer than β - and γ -males.

The half-molted female introduced to an α -male, a β -male, a γ -male, and another α -male, mated with all four males in rapid succession. Copulation in the first three cases proceeded normally. In the last case, the α -male ejaculated, but was apparently unable to place all of his ejaculate into the female's genital pores. Several sperm bundles were observed trailing out of the female across her ventral pereon after the last male released her. Copulations with all four males occurred within 30 min, and, within 5 min of the final mating, the female shed her anterior cuticle and began transporting ova into her brood pouch. Thus female receptivity lasts from moments after females shed their posterior cuticle until moments before the anterior cuticle is shed. During this time, females evidently will mate with any nearby male.

Discussion

Although premolt females are attracted to spongocoels containing α -males and engage in courtship behavior (*i.e.*, premolt females are behaviorally receptive, Shuster, 1986), the genital pores of premolt females are indistinct, and the oviducts of these females do not contain sperm. Actual sexual receptivity and copulation occur only in half-molted females, substantiating observations by Menzies (1954) and Ridley (1983). Females seem capable of postponing receptivity if males are not available. This is reasonable for a species in which females must leave the habitat in which they mature to locate suitable reproductive habitat (Shuster, 1986). However, females cannot postpone their reproductive molt indefinitely even when isolated from males, and once females molt, the presence of α -males does not affect the duration of receptivity. While receptive, however, females will mate more than once and with more than one male.

Females transport ova to their brood pouches almost

immediately after shedding the anterior portion of their cuticles, and females are sexually receptive until moments before this molt. Fertilization may occur in the ovary, as sperm tails, minus their acrosomes, were abundant in spent ovaries. Within the oviduct, sperm are non-motile, and while females may induce an acrosome reaction that initiates syngamy (P. Talbot, pers. comm.), this reaction is unlikely to propel sperm the length of the female reproductive tract. Females appear to possess contractile tissues in their oviducts that may facilitate sperm transport. Fertilization evidently does not occur in either the marsupium or in the oviduct itself, as has been suggested for some isopods (Ridley, 1983).

Females exhibit a single 24-h period of sexual receptivity. This interval seems somewhat brief until the potential density of competing males in a spongocoel is considered. Although most occupied spongocoels contain a single α -male, up to eight α -, β -, and γ -males in various combinations may simultaneously occupy the same spongocoel (Shuster, 1987a; 1989). At such male densities, 24 h of sexual receptivity introduces a high probability of multiple insemination for females, and thus presents considerable opportunities for sperm competition among males. Although it may be physically impossible for *P. sculpta* females to complete the two phases of their reproductive molt in less than 24 h, other isopod females complete their reproductive molts in a few hours or less (Ellis, 1971; review in Ridley, 1983). Furthermore, uniphase molting (*i.e.*, shedding of the entire cuticle at once) occurs in some marine isopoda (George, 1972). The possibility must therefore be considered that *P. sculpta* females somehow benefit from a period of sexual receptivity that is sufficient in duration to permit multiple mating.

All three male types performed similar activities associated with the act of copulation and the transfer of sperm. Intromission durations among the three male morphs were also similar and were consistently rapid (the transfer, within 30 s, of several hundred 1-mm-long sperm by males no larger than 7 mm in length is an amazing feat by any standard). Furthermore, the fecundities of females mated to α -, β -, and γ -males are not significantly different (Shuster, 1986; 1989).

Despite these similarities, the amount of time males spent with individual females differed significantly among males. Alpha-males retained females for some time after mating, while β - and γ -males released females immediately. This result makes sense given descriptions of the behavior and distribution of β - and γ -males in spongocoels (Shuster, 1986, 1987b, 1989). Beta- and γ -males seem well-adapted as sperm competitors (Shuster, 1987b, 1989) and could maximize their contacts with females by avoiding post-copulatory guarding (Parker, 1974). However, the fact that α -males release females at

all before females complete their reproductive molt is surprising. If females may be inseminated by other males, α -males have little to gain by releasing their half-molted mates unless other females are present.

In the field, α -males are often found gripping premolt or half-molt females with their walking legs (Shuster, 1986, 1987a). Furthermore, when single, receptive females are present in spongocoels with both an α -male and a γ -male, γ -males rarely mate successfully, suggesting successful post-copulatory guarding by α -males (Shuster, 1989). Perhaps in a watchglass and in the absence of other males, α -males are not stimulated to retain their mates. Observations of the copulatory behavior of these isopods within the confines of their natural reproductive habitat, as well as further analysis of patterns of female sexual receptivity in this species, may explain these apparently conflicting patterns of male guarding behavior and fertilization success.

Acknowledgments

I am grateful to Drs. Roy L. Caldwell, Frank A. Pitelka, Vincent H. Resh, George K. Roderick, and Eldridge S. Adams III for their comments on earlier drafts of the manuscript. Logistical support for this research was provided by Mona Radice and Mable Lee of the Department of Zoology, University of California, Berkeley, the Center for the Study of Deserts and Oceans in Puerto Peñasco, Sonora, Mexico, and the Environmental Research Laboratory in Tucson, Arizona. Financial assistance was provided by the Theodore Roosevelt Memorial Fund, and NSF dissertation improvement grant OCE-8401067, as well as by the University Regents' Fellowship, the Alice Galloway Memorial Fund, the Graduate Student Research Allocations Fund and the Departments of Zoology and Genetics of the University of California, Berkeley.

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